SILVERSIDE DIETS AND POTENTIAL COMPETITION IN THE TENNESSEE-TOMBIGBEE WATERWAY: THE INVASIVE *MENIDIA AUDENS* VERSUS THE NATIVE *LABIDESTHES SICCULUS*

A Thesis

by

KYLE RUBY STRONGIN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2009

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	William H. Neill
Committee Members,	Christopher M. Taylor
	Frances Gelwick
	Mary K. Wicksten
Head of Department,	Thomas E. Lacher

May 2009

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ABSTRACT

Silverside Diets and Potential Competition in the Tennessee-Tombigbee Waterway: The Invasive *Menidia audens* versus the Native *Labidesthes sicculus.*

(May 2009)

Kyle Ruby Strongin, B.S., Texas A&M University

Chair of Advisory Committee: Dr. William H. Neill

I investigated dietary differences, overlap and shifts for two atherinid fish species inhabiting the highly modified Tennessee-Tombigbee Waterway (TTW) in Mississippi, U.S.A. The Mississippi silverside (*Menidia audens*) is now common throughout the waterway and apparently invaded from the Tennessee River after man-made connection with the Tombigbee River in the mid 1980s. A subsequent decline in the distribution and abundance of the native brook silverside (*Labidesthes sicculus*) led to speculation that dietary competition might be involved. I used extant data to test the null hypotheses that diets are not different between the two silverside species in TTW, that dietary overlap between them is random and that no dietary niche shift occurs for either species in the presence or absence of its putative competitor. I accomplished this by quantifying the diet of both species from sympatric and allopatric collections, then using multivariate statistics and null models to test for significant dietary differences, overlap, and niche shifts. The analysis indicated that diets differed significantly between the two species. However, dietary overlap at sites of co-occurrence was greater than expected under conditions of

incipient competitive exclusion; and, dietary niche shifts were not found when the diet of either species in allopatric collections was compared to its diet in sympatric collections. Thus, there was no evidence for direct involvement of dietary competition in the population trends of silversides in the Tennessee-Tombigbee Waterway. Yet, it appears that *M. audens* is replacing *L. sicculus* in dominant habitats of TTW, just as has happened in other, similar systems. Simulations with STELLA® were used to estimate the degree of inter-specific competition that might account for observed rates of replacement. Results implied a 10 % ecological advantage of *M. audens* over L. *sicculus.*

ACKNOWLEDGEMENTS

I thank my committee chair, Dr. Neill, and my committee members, Dr. Taylor, Dr. Gelwick, and Dr. Wicksten, for their guidance and support through the various phases of my graduate program. Without their patience and understanding of the miles between us, this thesis would not have been possible.

Thanks also go to my friends and to the faculty and staff at Texas A&M University for making my time there such a great experience. I also thank the members of the faculty, staff and students of Mississippi State University for the help and guidance they provided. A special note of thanks goes to Dr. Phillip Bettoli, Tennessee Cooperative Fishery Research Unit, Tennessee Tech University, for providing data from his study of silverside population trends in Lake Conroe, TX.

Finally, I thank my mom and dad for all the love and support they have provided me. To my husband, I give thanks for the encouragement, patience and love he has shown throughout this process.

NOMENCLATURE

L. sicculus	*Labidesthes sicculus,* the brook silverside
M. audens	*Menidia audens,* the Mississippi silverside
M. beryllina	*Menidia beryllina,* the inland silverside
MRPP	Multiple Response Permutation Procedure
NMS	Nonmetric Multi-Dimensional Scaling
STELLA	Proprietary computer program for simulation modeling. The program is marketed by iSee Systems, Inc., Lebanon, NH.
TTW	Tennessee-Tombigbee Waterway; also, known as “Tenn Tom”

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INTRODUCTION

Reservoirs constructed on major rivers throughout the United States have led to extreme changes in the fish communities of the affected watersheds (Lienesch et al. 2000; Martinez et.al. 1994) due to drastic and irreversible habitat alterations (Boschung 1987). The Tennessee-Tombigbee Waterway (TTW; also, Tenn Tom) was created by the U.S. Army Corps of Engineers, between 1972 and 1985, to connect the Tombigbee River with the Tennessee River system for shipping purposes (Figure 1). The development of this waterway greatly changed the physiography of the upper Tombigbee River. The river has become fragmented, and flows are controlled by waterway operations at minimum-flow-control stations (Figure 2; Taylor et al. 2008). This change in flow regime has caused marked seasonal changes in the high and low water marks. In the Tennessee and Tombigbee drainages, what had been lotic habitat ideal for native stream fishes became predominately a lentic system, maintained by a series of locks and dams. Fragmentation of the system isolated tributaries and their fish populations.

There also have been conspicuous changes in the aquatic-community assemblage present in the former Tombigbee River. In particular, the connection of the Tombigbee River to the Tennessee River, creating the Tennessee-Tombigbee Waterway, has allowed the invasion of the Mississippi silverside *Menidia audens* from the Mississippi River system (Taylor et al. 2008); before, only the brook silverside *Labidesthes sicculus* had been present. After the waterway's construction, the non-native Mississippi silverside

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This thesis follows the format of the journal Ecology of Freshwater Fish.

invaded the system and its distribution began to overlap that of the native brook silverside. A recent survey of upper portions of the Tenn Tom has indicated that now *L. sicculus* and *M. audens* both are commonly encountered throughout the system, with a tendency toward replacement of *L. sicculus* in the more lentic habitats by *M. audens*.

Previous invasions of such habitats by *M. audens* have led to a documented decrease in *L. sicculus* numbers (Pratt et al. 2002). In Lake Texoma, Oklahoma, *L. sicculus* was the only silverside encountered until 1953, when a small population of *M. audens* was first reported (Riggs & Bonn 1959). By 1955, dense aggregations of *M. audens* were being reported and an apparent decline in the numbers of *L. sicculus* was observed (Hubbs 1982). The mechanisms of species interaction that would account for the apparent negative association between species are not clear, but one possibility is habitat-dependent competition for food.

Until the creation of the Tenn-Tom waterway, *M. audens* was not observed to inhabit the upper Tombigbee River, now part of the TTW. Because *M. audens* and *L. sicculus* now co-inhabit certain regions of the TTW, it is important to document distributional trends and to seek evidence of species interactions that might portend eventual displacement of the brook silverside by the Mississippi silverside. I analyzed existing fish collections and associated records at Mississippi State University, to assess temporal and spatial trends in distribution and relative abundance of the two silverside species. For representative collections, the stomach contents of silversides were examined to assess the composition of the diet. The extent of dietary overlap for collections in which the two species co-occur was estimated, and diets were compared for each species between collections in which the other species was present and those in which it was not. Finally, information from the literature was used to parameterize a

simple model for simulating population dynamics of two potentially competitive species, and the model was applied to project time to replacement of brook silverside by Mississippi silverside in TTW.

MATERIALS AND METHODS

The study was conducted over a four-year period, with samples collected from various locations in the Tennessee-Tombigbee Waterway from 2002 through 2006. Data were obtained from locations where *Labidesthes sicculus* and *Menidia audens* were sympatric and allopatric to evaluate potential dietary overlap and shifts. The 39 locations ranged from Aberdeen, MS, south to Columbus, MS (Figure 3). Fishes were collected using 1.8- by 6.1-m, 4.8-mm mesh seine, and each site was sampled for an hour. Previous sites of known occurrence for *M. audens* and/or *L. sicculus* were included among sampling locales. The stream width and current velocity were measured at each site. These measurements were used for comparison of environmental variables that may have affected relative abundance of the two silverside species, or availability of forage items.

Dissections were performed on at least 10 silversides of each species collected at sampling sites. Randomly selected individuals, both from historical and current collections, were analyzed for diet composition as indicated by stomach contents. Fish had been preserved in a 70% ethanol solution until analysis was performed. Fish were measured, and dissected with the aid of dissecting microscope. The stomach from the posterior end of the esophagus to the origin of the small intestine was removed. Stomach contents were removed and analyzed by identifying specimens to the most restrictive taxonomic group possible, with aide of taxonomic keys for unknown species. The diets of the two silverside species then were compared and analyzed for any similarities/differences using PCord (MjM Software 2006) and Systat (Aspire Software) statistical software.

Nonmetric Multidimensional Scaling (NMS) was used to compare the diets of the two species and for each species in sympatry versus allopatry. The diet-item counts were

square-root transformed and analyzed utilizing the Sorenson distance measure. NMS is an ordination method used in community ecology to order specific sampling units based on abundance and occurrence (Ludwig & Reynolds 1998). The algorithm maximizes the correlation between distances in ordination space and the original data matrix (McCune et al. 2002). Distance in ordination space represents the dissimilarity between measured sampling units. Total stress calculated for the data is representative of the monotonicity within the data, where a stress value of zero is considered completely monotonic. In this study, distances between sample units plotted in ordination space correspond to the degree of dietary dissimilarity present between the two species and, within species, between individuals in sympatry versus allopatry.

Indicator species analysis (ISA) (Dufreˆne & Legendre 1997) was used to identify diet items important in discriminating between the two species. This method combines information on abundances and occurrences to produce indicator values ranging from zero (no indication) to 100 (perfect indication), which then were tested for statistical significance with a Monte Carlo randomization procedure (5000 randomizations).

The Multiple Response Permutation Procedure (MRPP) was applied to compare the pair-wise and across-group similarity of diets between the two silverside species. Unlike parametric tests used for this purpose (e.g., discriminant function analysis), MRPP makes no distributional assumptions (Smith 1998). When MRPP is used in conjunction with NMS, it is recommended that the same distance measure be maintained across analyses (McCune et al. 2002). Thus, my data were square-root transformed prior to analysis with the Sørensen distance measure. Probability of a type I error was calculated with a randomization algorithm that allows for comparison between an observed (weighted mean within-group distance) and the randomized distribution. This probability

value expresses the likelihood of generating a random number smaller than the observed value. An effect size "A" also can be calculated and represents the "chance corrected within-group agreement" (McCune et al. 2002), a measure of observed within-group homogeneity relative to what can be expected by chance. Within-group homogeneity is greater than the random observation when $A > 0$ and less when $A < 0$. The A-value is useful in attaching ecological significance to observed differences among groups because it is independent of sample size (Mielke 1984, McCune et al. 2002).

An ANOVA was performed on stream width and velocity variables for locations where each species occurred in allopatry. This was done to determine if either of these variables were significant when observing habitat preferences which existed among the assemblages of the two species.

A null-model approach was used to assess dietary overlap; for this, I used Ecosim (Gotelli & Entsminger 2009). A randomization algorithm (1000 randomizations) that retained niche breadth and zero states was used (Gotelli & Graves 1996). Overlaps were calculated with Pianka's method. This method considers the abundance of dietary items collected from the two species and analyzes probability of observed diets occurring, based on chance.

Competition modeling was performed, using STELLA® software (iSee Systems, 2004), to simulate the joint temporal trends in relative abundance of *L. sicculus* and *M. audens* in situations similar to that in the TTW system. STELLA is a systems-simulation program that allows the user to simulate processes based on finite-difference equations that describe dynamics of the system being represented (Costanza & Vinov 2001; iSee Systems, 2004). Estimates from previous research and life history of both species were used to analyze how the ecological overlap between the two species and their respective

turn-over rates might affect population trends in TTW. Simulated time-rate of population change for each species assumed the theta-logistic function, with theta = -5, which seems the characteristic value for fishes (Sibley et al. 2005):

dNi/dt = -ri*Ni*(1-(effectiveNi/Ki)^-5),

with r = 1.9/yr (0.158/mo) for each species and K = 100 units for each species. The value of r, the coefficient for population flux, or turn-over, was fit by trial-and-error to data provided by Dr. Phillip Bettoli (Tennessee Cooperative Fishery Research Unit, Tennessee Tech University; pers. comm.) and is consistent with observations on silverside population dynamics in Lake Conroe, TX (Bettoli et al. 1991). K is relative "carrying capacity" and was set arbitrarily to 100 units for each species. The variable "effectiveNi" is the sum of Ni and the ecologically-equivalent number of the other species, Nj. Step-time (STELLA's DT) for simulations was 1 month; duration of simulations was 144 months.

RESULTS

Results from the NMS ordination (Figure 4) documented dietary differences between species and between individuals within each species at sites of sympatry and allopatry. The results showed that there was more similarity between the diets than would have been expected by chance. Axis 1 accounted for 25.7% of data variance and axis 2 accounted for 39.6% of data variance. Total stress for this analysis was 22.7.

Indicator species analysis was performed on diet items collected from each species. *Daphnia lumholtzi* was a strong indicator across all samples of *M. audens* diets.

Results of MRPP analysis indicated that the measured dietary differences among groups of the same species were not statistically significant: *M. audens* diets at all locations, A=0.008, P=0.246; *L. sicculus* diets at all locations, A=0.007, P=0.664. However, the diets of *L. sicculus* and *M. audens* were found to be statistically different: A=0.059, P<0.001.

Result from ANOVA showed a significant difference for two environmental variables representative of habitats where each species is commonly collected. Mean stream width for *Labidesthes* was much narrower at 26.8m, compared with that of *Menidia* at 123.1m; measured p-value was 0.001. Mean current velocity for *Labidesthes* was measured at 0.62m/s, compared with that of *Menidia* at 0.11m/s; representative of the difference between lotic and lentic habitat preference with a p-value of 0.005.

Ecosim results indicated that overlap of sympatric and allopatric *L. sicculus* was not significantly less than expected based on chance (observed overlap = 0.687, mean of simulated overlaps = 0.471, P = 0.921). Thus, no dietary shift was evident when *M audens* was present versus absent. Nor did sympatric and allopatric *M. audens* show a dietary shift (observed overlap = 0.714, mean of simulated overlaps = 0.280, P = 0.994).

When comparing the diets of sympatric *L. sicculus* and *M. audens,* overlap was high with no evidence of dietary segregation (observed overlap = 0.781, mean of simulated overlaps = 0.0.356, P = 0.998)

The STELLA® model for simulating co-dependent population dynamics of two species is presented in Figure 5. Simulations suggested that shared resource use between the two silverside species need overlap only by about 10 %, in favor of *M. audens*, to account for the rate of replacement of *L. sicculus* by *M. audens* observed by Bettoli et al. (1991) in Lake Conroe, TX (Figure 6). The requisite model assumed equal rates of intrinsic population flux, 1.9 per year (= 0.158/month), which seems generally consistent with silverside biology (Hubbs 1921; Wallus & Baker 2006). With N1 and N2 representing relative abundances of *Labidesthes* and *Menidia*, respectively, goodness-of-fit between modeled and observed silverside population trends in Lake Conroe seemed maximal when effectiveN1 was set = N1 + 1.1*N2, and effectiveN2 was set = N2 + 0.9*N1. Data collected from 2002 through 2006 in the TTW show a steady decline in the abundance of *L. sicculus* relative to that of *M. audens*. The average catch of *L. sicculus* to *M. audens* during this time period was 1:3. Under the model parameterized for the Lake Conroe, TX, scenario, this would indicate that extirpation of *L. sicculus* from TTW may occur sometime before 2015.

DISCUSSION

The difference observed between the diets of *M. audens* and *L. sicculus* was greater than expected by chance, but no detectable dietary shift has occurred thus far between the two species in TTW. ANOVA results show that dietary preferences of the two species are likely related to environmental variables, especially stream width and velocity, rather than to competition for food. Analysis of occurrence data by habitat suggests that *L. sicculus* prefers lotic areas, such as tributaries, or coves and waterway confluences with tributaries ; whereas, *M. audens* prefers lentic habitats including reservoirs and the waterway. *M. audens* and *L. sicculus* have been found to co-inhabit the areas where these two habitats converge. The creation of the Tenn-Tom Waterway may have pushed *L. sicculus* out of its natural habitat into more upstream/side-channel locations. Construction of a reservoir has been shown to act as a barrier to potential colonizers living in adjacent creeks and the flowing portion of the impounded river (Lienesch et al. 2000).

Inter-specific competition has often been implicated as occurring between *L. sicculus* and *M. beryllina* (the latter probably synonymous with *M. audens*; see Suttkus &Thompson 2002) because introduced inland silversides have rapidly displaced endemic brook silversides in some reservoirs. The brook silverside was living in tributary streams of Lake Texoma prior to impoundment (Sisk & Stephens 1964) and was the only silverside in the reservoir until 1953 (Moore & Buck 1953; Riggs & Dowell 1956). The inland silverside was first discovered in the Red River drainage in 1949 (Moore & Cross 1950) and in Lake Texoma in 1953 (Riggs & Bonn 1959), but was not common in the lake until the summer of 1954 (Riggs & Dowell 1956). By 1955, the native brook silverside was found only in Lake Texoma's tributaries (Riggs & Dowell 1956; Saunders

1959). Samples collected in Lake Texoma from 1957 and 1958 showed that *Menidia* was the only silverside inhabiting the reservoir (Riggs & Bonn 1959).

Previously reported observations on silverside population trends in Lake Conroe, TX (Bettoli et al. 1991; P. Bettoli pers. comm.), have enabled parameterization of a speculative model for simulating co-dependent population dynamics of the two silverside species. In the STELLA® modeling exercise, I assumed equal intrinsic rates of population flux. I then estimated the degree of competitive overlap required to generate observed population trends ending in extirpation of *L. sicculus* by *M. audens* in Lake Conroe. Results suggested that one unit of *M. audens* is ecologically equivalent to about 1.1 units of *L. sicculus.* The compliment of this is that 1 unit of *L. sicculus* is equal to about 0.9 units of *M. audens.* This relationship was used to drive population trends of the two species, suggesting that *M. audens* tends to replace *L. sicculus* within about a dozen years after first contact in lentic systems. Given *M. audens* already has a 3:1 advantage over *L. sicculus* in TTW, complete replacement of the native by the invading silverside may be expected by about 2015.

Because the diets of silversides I studied were so similar, I believe that the observed success of *Menidia* in invaded systems like TTW is due to its ability to better utilize the lentic habitat and its resources overall. Important to this presumptive competitive advantage of *M. audens* over *L.sicculus* is a difference in prey-attack strategy. Relative capture success has been studied for the two species in varied environments. As individual size increases, *Menidia* has a more protrusible mouth, but protrusiblilty of *Labidesthes'* mouth decreases with size. This allows for a shorter attack time and distance for *Menidia,* when feeding on cladoceran prey like those that have come to dominate the TTW. In such situations, *Menidia* tends to be more successful than

Labidesthes in capturing a larger variety of prey items (McComas & Drenner 1982). This difference in prey-capture mechanics, combined with the similarity of the species' prey preferences, may lead to differential rates of feeding effectiveness when both species are present in a system.

Historical data suggest that *L. sicculus* had remained fairly stable in the Tenn-Tom system prior to appearance of *M. audens* (Unpubl. data, Miss. Fish and Wildlife Dept.). The data from previous studies have shown that once *M. audens* enters a system, replacement of *L. sicculus* is common (Riggs & Dowell, 1956; Riggs & Bonn, 1959; Bettoli, et al. 1991). Under ecological conditions like those of TTW, the potential competitive advantage provided by the prey-attack strategy in *M. audens* may be key. Further studies need to be conducted in the Tenn-Tom system to monitor population trends that may document possible replacement of *L. sicculus* by *M. audens,* and other changes in the ichthyofauna and its forage base.

SUMMARY AND CONCLUSIONS

1. *Menidia audens* seems to be replacing *Labidesthes sicculus* in the Tennessee-Tombigbee Waterway (TTW), just as it has in other, similar situations.

2. This may be due to the observed difference in environmental parameters and the presumed difference in prey-attack mechanics, leading *M. audens* to be able to better compete for forage than *L. sicculus* in lentic systems.

3) However, my study provided no clear evidence that *M. audens* is out-competing *L. sicculus* for preferred types of food in TTW:

a) The two silversides ate somewhat different forage items, but where they co-occurred, their diets overlapped broadly.

b) There was no evidence of forage shifts at sites of co-occurrence relative to sites of non-co-occurrence, for either species.

4) Simulation modeling suggested that the competition may be more quantitative than qualitative: Co-dependent population dynamics, favoring *M. audens* by only about 10 %, could account for the observed rate of replacement of *L. sicculus* by *M. audens* in L. Conroe, TX.

5) Extrapolation of the 2002 through 2006 average (1:3) relative abundance ratio in TTW under the same model suggests virtual extirpation of *L. sicculus* by *M. audens* in TTW by the year 2015.

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APPENDIX

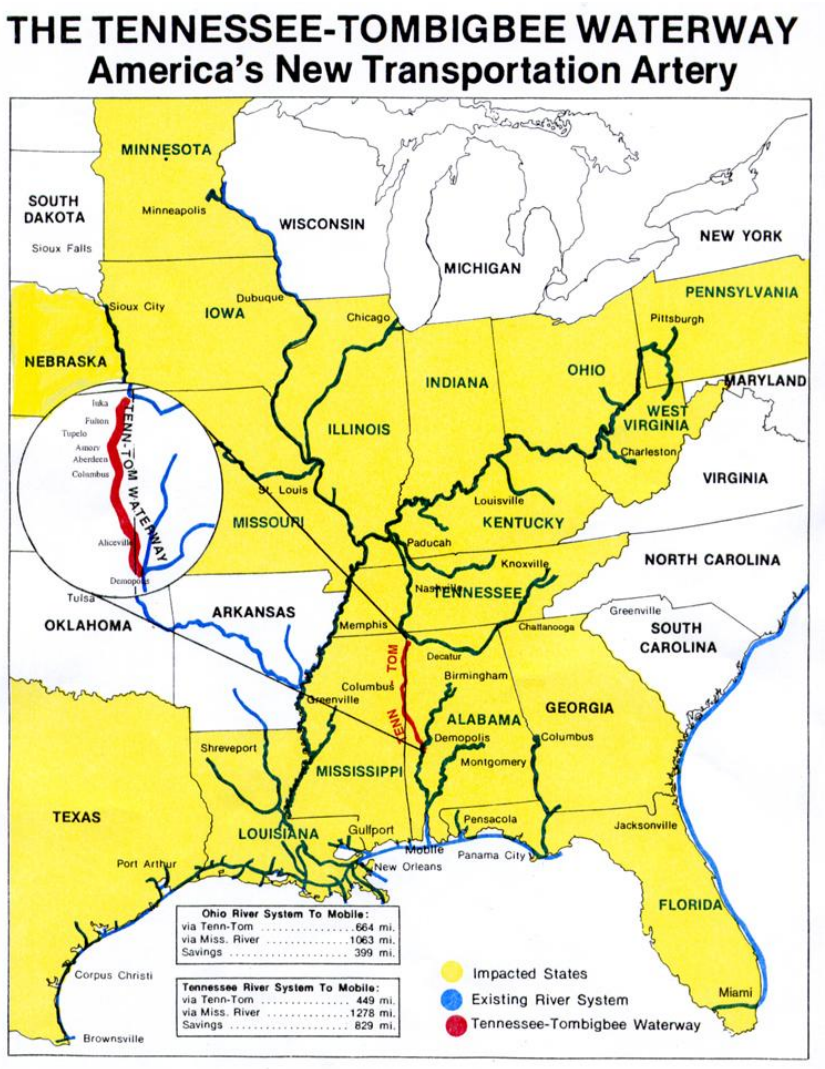

Figure 1. Map of the southeastern USA, showing location of the Tennessee-Tombigbee Waterway. The "Tenn-Tom" connects the Tennessee River to the Tombigbee River in northeastern Mississippi and northwestern Alabama.

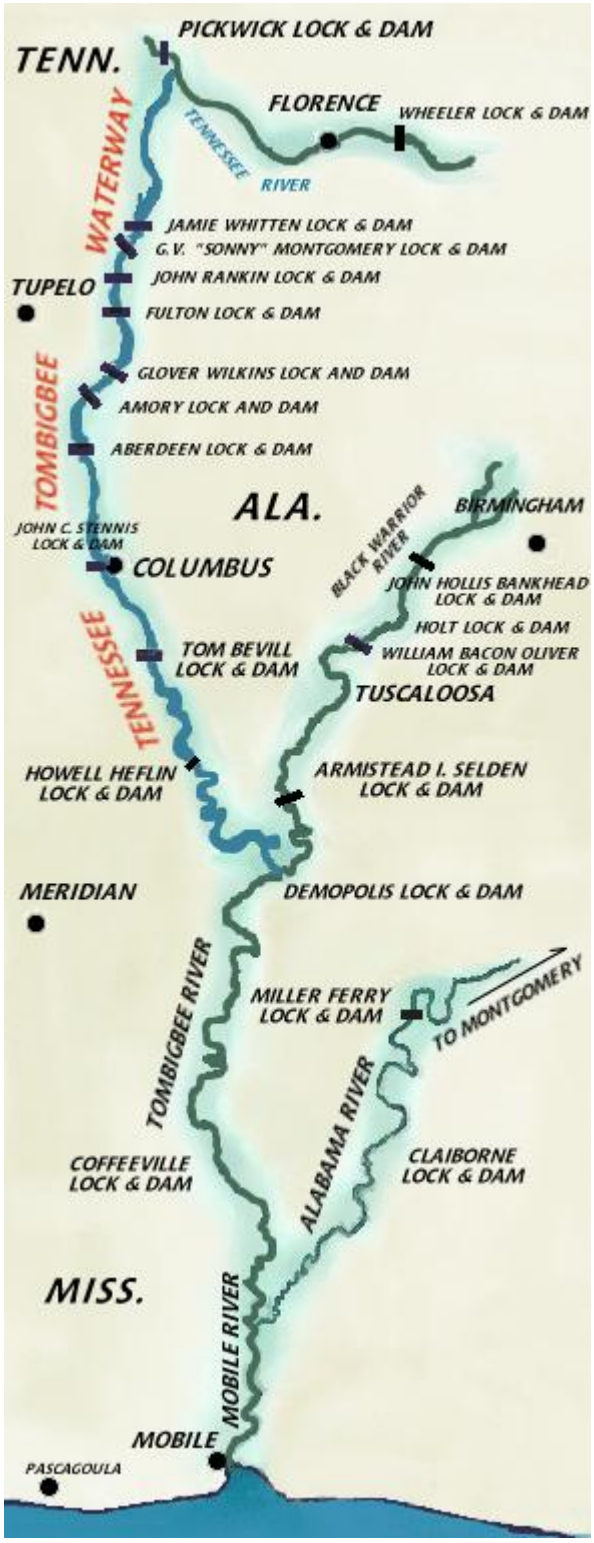

Figure 2. Detailed map of Tennessee-Tombigbee River including lock and dam systems now regulating flow regimes of the lower Tombigbee River drainage basin.

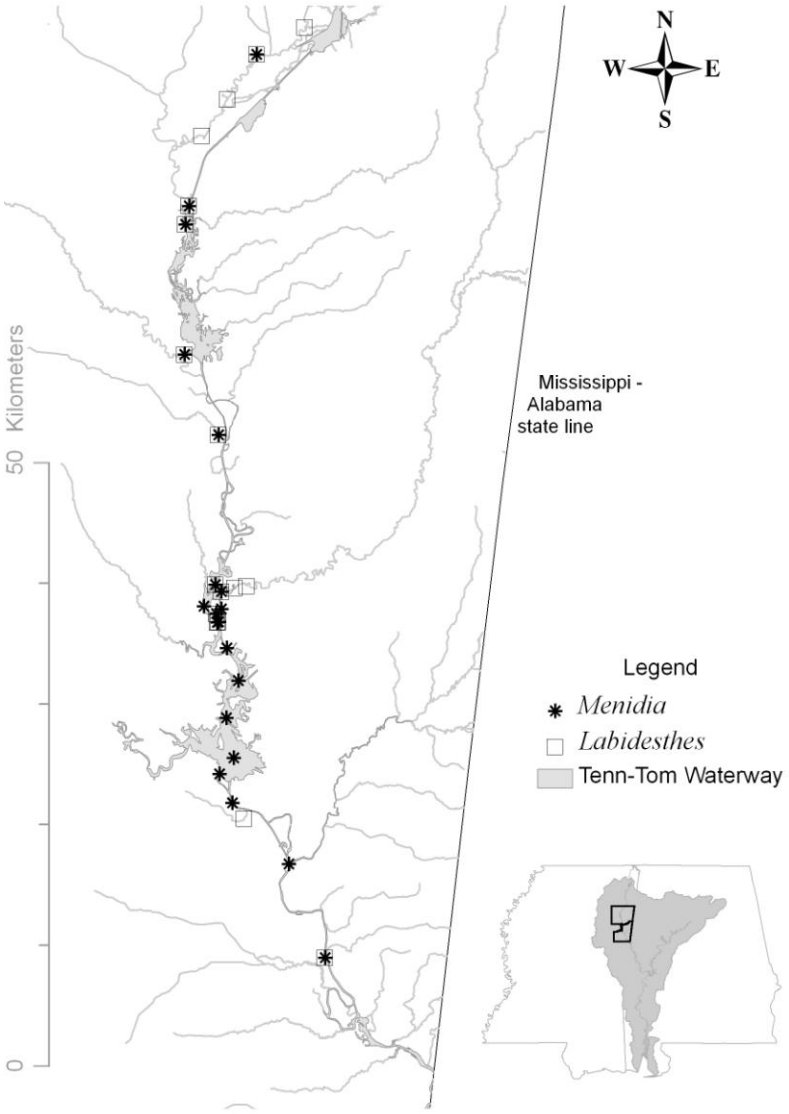

Figure 3. Collection sites for samples of *M. audens* and *L. sicculus*. Sites with stars represent collections of *M. audens*; sites designated by boxes represent collections of *L. sicculus*.

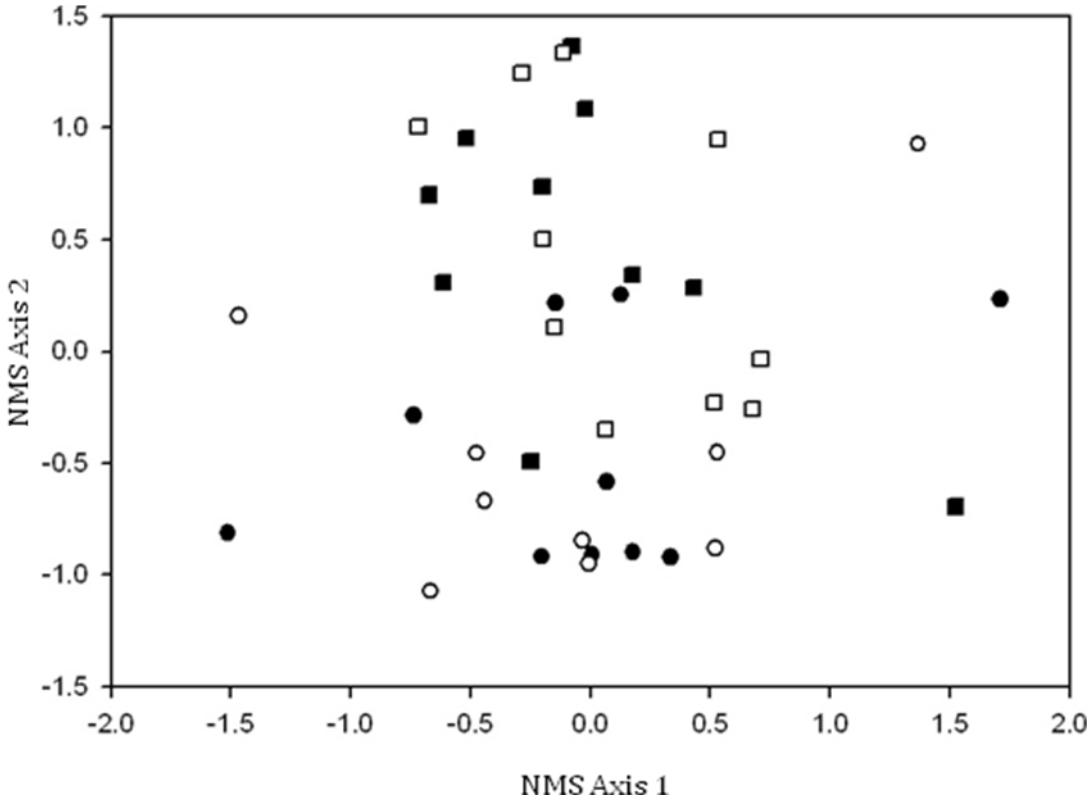

Figure 4. Nonmetric Multidimensional Scaling of diet use for *M. audens* and *L. sicculus*. Circles represent *L. sicculus* and squares represent *M. audens.* Closed symbols indicate sites of sympatry and open symbols indicate sites of allopatry. Observed distances are representative of differences in collected diet items.

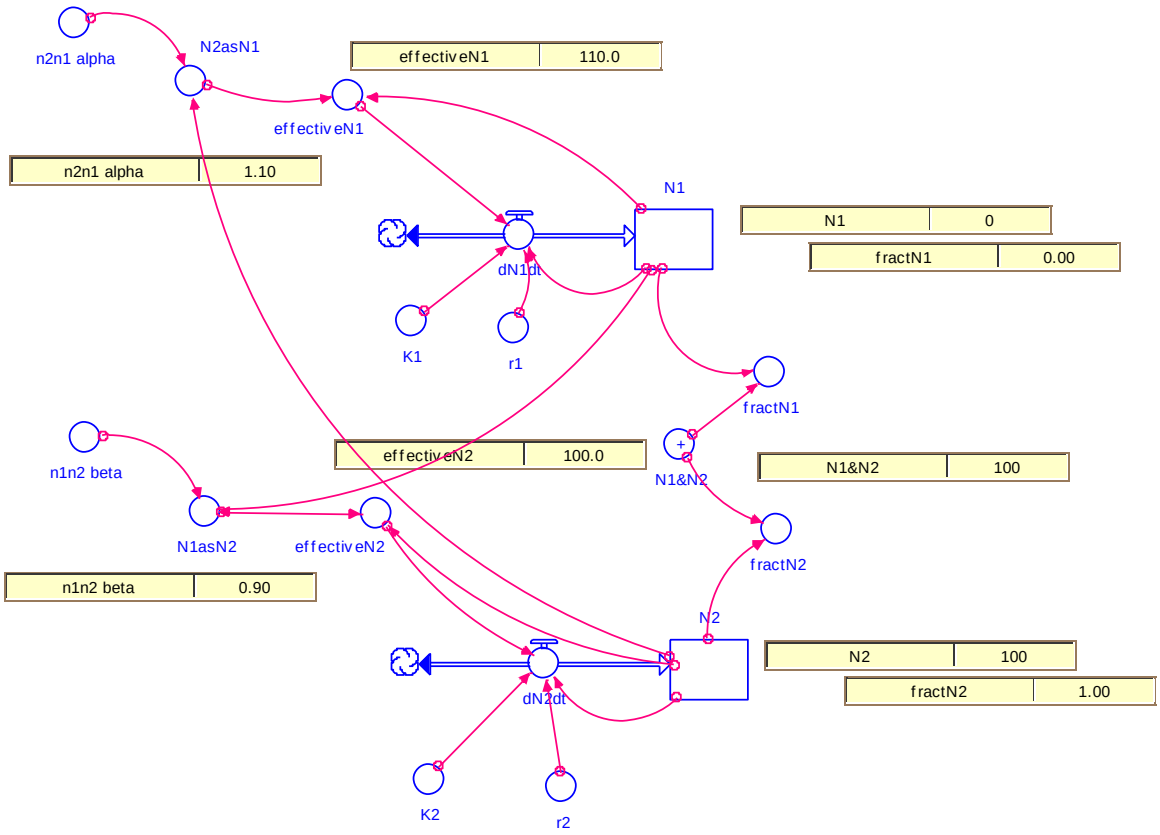

Figure 5. Diagram of STELLA model for simulating co-dependent population dynamics of two potentially competing species. Species 1 is representative of *L. sicculus* and species 2 is representative of *M. audens.* Alpha and beta values represent similarity between the two species, a value of 1.0 indicating complete equivalency and 0.0 indicating complete independence. Values of r were based on previously studied rates of population change (Bettoli et. al 1991). Initial values of N1 and N2 were set at 98 and 2, respectively, to simulate invasion by species 2 into a system initially dominated by species 1. Fractional values of each species at end of the 144-mo simulation show a complete extirpation of *L. sicculus*.

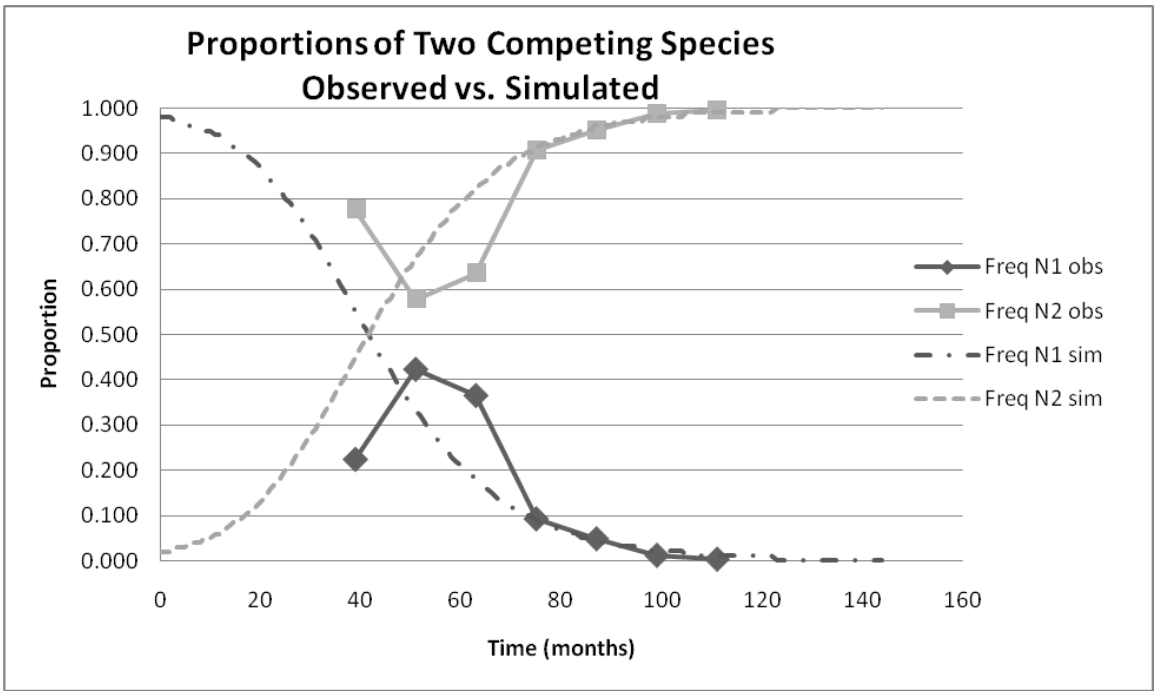

Figure 6. Relationship between observed proportions of *L. sicculus* (fractN1) and *M. audens* (fractN2) in Lake Conroe, TX (Bettoli et. al 1991), and values obtained via STELLA® simulation. Observed and simulated series were matched starting at month 38, which corresponded with the year 1980 in Lake Conroe.

Table 1. Nonmetric Multidimensional Scaling analysis of diet contents for *M. audens* and *L. sicculus* collected from the Tennessee-Tombigbee Waterway, 2002-2006.

Species	NMS Axis Correlations		Indicator Species Analyses		
	Axis 1	Axis 2	Indicator Value (IV)	Mean Random IV	p-value
Daphnia lumholtzi	-0.087	0.762	62.3	28.2	<0.001
Daphnia sp.	0.263	0.201	48.4	26.6	0.008
Empididae	0.122	-0.508	47.8	39.4	0.092
Amphipoda	0.043	0.074	5.0	5.1	1.000
Anostraca	-0.182	0.187	18.3	12.2	0.156
Mymaridae	0.055	-0.025	6.3	8.7	0.862
Culicidae	0.348	0.010	6.1	10.2	0.803
Ostracoda	0.161	0.079	15.0	8.8	0.226
Argulus	0.118	0.156	20.0	10.3	0.100
Calonoida	0.112	0.094	10.0	6.6	0.494
Cyclopoida	-0.145	0.087	20.1	14.2	0.146
Conchostracha	-0.108	0.110	17.5	12.3	0.197
Gammaridae	0.094	0.097	20.0	10.3	0.109
Gerridae	-0.378	-0.354	16.9	12.1	0.248
Halellidae	0.124	0.174	25.0	12.3	0.048
Perlodidae	0.096	-0.331	15.8	8.8	0.110
Arachnida	-0.007	-0.033	14.5	16.4	0.698
Nematocera	0.175	-0.156	7.8	8.7	0.610
Larval Fish	0.107	0.282	26.7	15.2	0.050
Ceratopogonidae	-0.145	0.287	33.8	24.8	0.125
Ephemeroptera	0.130	0.206	5.0	5.1	1.000
Leptophlebiidae	0.257	-0.155	10.7	15.2	0.922
Diptera larva	-0.176	-0.189	9.0	8.8	0.351
Ascaris sp.	-0.135	0.378	25.0	12.1	0.046

VITA

Name: Kyle Ruby Strongin

Address: Department of Wildlife and Fisheries Sciences
210 Nagle Hall
2258 TAMU
College Station, TX 77843-2258

Email Address: kstrongin04@hotmail.com

Education: B.S. Marine Biology and Biomedical Science, Texas A&M University, 2005

Employment: University of South Carolina
Department of Biological Sciences
715 Sumter Street
Columbia, SC 29208

Central Carolina Technical College
Department of Health Science and Nursing
506 N. Guignard Drive
Sumter, SC 29150